

## Fossil Mammals of Africa

No. 4

# MIOCENE ANTHRACOTHERIIDAE FROM EAST AFRICA 

## BY

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With four plates and two figures in the text

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## Introduction

The material to be described in this paper comprises the bulk of the Miocene Anthracotheriidae collected by members of Dr. L. S. B. Leakey's archaeological expeditions during 1932, 1935, and I94I, supplemented by specimens obtained by the late Archdeacon Owen during the same period, and by the British-Kenya Miocene Expedition of 1947. The entire collection of Anthracotheres from these expeditions is at present housed in the Coryndon Memorial Museum, Nairobi. I am indebted to the Government Grants Committee of the Royal Society, whose financial assistance made much of the collecting possible, and also to Dr. Leakey and to the late Archdeacon Owen, for placing their material at my disposal. I wish also to record my most sincere appreciation of the invaluable help and advice given me by the late Sir Clive Forster Cooper in the preparation of this paper.

The area from which these collections were obtained lies immediately south of the equator, between $0.0^{\circ}-2 \cdot 0^{\circ} \mathrm{S}$. and $33 \cdot 0^{\circ}-36^{\circ} \mathrm{E}$.

The Anthracotheriidae are not at present very well represented in the Miocene deposits of this part of East Africa, and with one notable exception most of the specimens are exceedingly fragmentary and indeterminate. Some material was collected from the Karungu beds in IgII by Felix Oswald; this was described by C. W. Andrews in I914, and included a new species Merycops africanus. Most of the material described in the present paper was obtained from the neighbouring deposits of Rusinga Island, and from Ombo, near the northern shore of the Kavirondo Gulf. The collection includes two genera, and it is possible that there may be several species amongst the indeterminate material. Unfortunately, however, the fragmentary condition of many of the specimens, particularly those from Ombo, and the state of wear of the teeth, renders exact comparison with other forms almost impossible; it has therefore been necessary to omit specific identification of all but the Rusinga specimens. The Ombo fragments appear to have closer affinities to the genus Hyoboops Trouessart than to any other, and they are therefore provisionally regarded as representing an indeterminate species of that genus.

In East Africa, the discovery of complete specimens of skulls, mandibles, or
limb-bones is rare, whilst complete skeletons, or associated skeletal material of anything but the larger animals, are almost unknown. This is probably due to the abundance of scavenging carnivores and crocodiles which effectively destroyed most of the animals that died either on the land surface or in the Miocene lake. The only two complete skeletons yet recovered from the Rusinga deposits have been those of Rhinocerotids. One of these had been exposed on the surface for some considerable time before discovery, and most of the bones were almost weathered away. In the second example, however, the skull, vertebrae, ribs and limbs of the lower side were almost wholly intact and articulated, whilst in the upper half the limbs had been torn off and discarded, though still almost completely articulated, within a few feet of the body. The ribs of the upper side had been forced forwards and backwards from a central point, indicating that the scavengers had penetrated the softer parts of the belly, but had apparently been unable to do any appreciable damage to bones of such bulk. In most of the smaller animals the preserved remains are not only isolated but fragmentary, and show fractures which were clearly made prior to deposition. In consequence, it is frequently impossible to make any direct comparison of fossils with previously described species from other parts of the world.

When dealing with new collections of fragmentary or isolated material, it is frequently found that the specimens do not agree exactly with previously described species, and it thus becomes necessary to determine whether the points of differences are to be regarded as specific, or whether the specimens should be included within the species which they most nearly resemble. This decision must inevitably depend purely upon individual opinion and preference. Since it is seldom possible to obtain long series of fossil species, it follows that we cannot determine the limits of individual variation which must be taken into consideration, and it is essential that material of doubtful relationship should be described for the benefit of other workers, without adding to the confusion by the formation of unwarranted new species.

The examples of Brachyodus described in this paper include specimens which show a marked similarity to those of B. africanus Andrews (I899) from the Lower Miocene of Egypt. Unfortunately the original material of the latter consists only of the mandible and lower dentition, which renders exact comparison of the Rusinga skull and upper dentition impossible. The lower teeth in the Rusinga collection show certain structural differences from those of Andrews' species, and for this reason they are separated from it as a distinct species. The Rusinga Island skull is taken as the holotype of the new species, although it was not found in association with the mandible fragments. Whilst it must be admitted that there is no definite evidence to associate the skull with the mandible fragments, there would equally be no justification for separating it as a distinct species, which would at least imply some good reason for disassociating the two specimens. In view of the fact that the bulk of the skulls, skull fragments and upper teeth indicate a single species, and all the fragments of mandible and lower teeth also appear to belong to a single species, it seems reasonable to refer them to the same form.

## Genus BRACHYODUS Depéret

Brachyodus aequatorialis sp. nov.

Pls. 1-3; 4, figs. I-3

Diagnosis.-A species of Brachyodus closely allied to B. africanus Andrews, with more brachydont cheek-teeth, and more complex enamel folding in the lower premolars.

Holotype.-A nearly complete skull (Pls. I and 2).
Horizon.-Lower Miocene.
Locality.-Rusinga Island, Central Kavirondo, Kenya Colony (Lat: $0^{\circ} 25^{\prime}$ S. Long: $34^{\circ}$ I2' E.).

Other Material.-Two fragmentary skulls; two pieces of a single mandible; some isolated fragments of mandible and of upper and lower teeth. In addition, some limb-bones and metapodials are provisionally included in this species, although not definitely associated with any of the other specimens.

## Description

Skull. The most complete skull lacks only the anterior part of the pre-maxillary area and the left zygomatic arch. There is very little distortion throughout, but the two fragmentary skulls are severely crushed and distorted; in one only the brain case is preserved, whilst the other has, in addition, part of the face and palate. Such teeth as remain, however, are extremely fragmentary in this specimen; only the inner borders of M. 2 and M. 3 on the left, and part of the protocone of M. 3 on the right side being preserved. The cusps are worn down almost to the level of the cingulum. The following detailed description of the skull is based primarily on the holotype.

The suture lines throughout are unfortunately very obscure, and innumerable fine cracks over the entire surface add to the difficulty of determining their exact position. The suture between the pre-maxilla and maxilla is obscured on the dorsal surface, though visible below, but it appears that the pre-maxilla extended far back, and came into contact with the nasals for about 25 mm . The anterior part of each pre-maxilla is broken, but the angle at which the outer margins of the two bones converge at the point of fracture suggests that some 60 mm . is missing. The bone of the left side is slightly the longer, and measures 140 mm . from the posterior extension of the nasal aperture to the point of fracture. Thus, if the length of the missing portion is correctly estimated, the nasal aperture must have measured about 200 mm ., practically one-third of the total length of the skull. The premaxillae form almost vertical walls bounding the nasal aperture laterally, whilst the floor of the aperture is almost flat. The anterior palatal foramina are broken through, but it is clear that they were in the form of long slits, separated by narrow bars of the pre-maxillae in the middle line. The posterior palatal foramina are also in the form of slits, measuring about 40 mm . in length, and are situated well forward; the posterior ends being level with the middle of Pm.I.

On the dorsal surface the nasal bones are complete, and measure 185 mm . in
length. Anteriorly they are tapered, and project over the nasal aperture for a distance of 50 mm . The maximum anterior breadth across the nasals-apparently at the point of contact with the pre-maxillae-is 65 mm . The suture-lines then appear to converge slightly for about 30 mm ., to a point at which the transverse breadth is 53 mm ., and they then diverge again to their extreme maximum breadth of 78 mm . From this point the lateral suture extends inwards and backwards in a straight line, to meet the median suture at an angle of about $25^{\circ}$. The posterior point of the nasals lies about 27 mm . behind a line joining the anterior borders of the orbits. There is a distinct depression of the frontal bones on either side, between the orbits and the proximal ends of the nasals.

The post-orbital process of the frontal is somewhat elongated, and projects downwards towards the zygoma, from which it is separated by a space of 34 mm . There appears to have been no corresponding upward process from the latter. The infra-orbital foramen is damaged in all three specimens, but it was clearly not so large as that of Bothriogenys, separated by Schmidt (1913, p. 157) as a subgenus on account of the very large size of this foramen. The crests showing the attachments of the temporal muscles are very well developed, beginning near the apices of the postorbital processes, and thence curving inwards and backwards, to meet at a point about 67 mm . behind the posterior margin of the orbits. From this point to the posterior border of the skull the sagittal crest measures 185 mm ., attaining a maximum height of 35 mm . From the posterior ends of the zygomatic arches sharp crests curve upwards and slightly outwards to unite the supra-occipital crest, and thence curve sharply inwards to meet in the middle line, thus forming a pronounced backward flange over the occipital region.

The exoccipital condyles are very large in proportion to the size of the occipital, and are separated laterally from the occipital crest by very deep pits. Posteriorly they are separated by deep valleys from the paroccipital processes, which again are separated from the post-glenoids by wide grooves, in which the tympanic necks can be seen.

The zygomatic arches arise, anteriorly, opposite to M.2-M.3, the anterior margin of the space enclosed by the arch being level with the middle of M.3. The dimensions of the space are $125 \mathrm{~mm} . \times 80 \mathrm{~mm}$. The lower surface of the sphenoidal portion of the arch is flat, and merges into the glenoid, the posterior edge of which curves sharply downwards at about $90^{\circ}$ to form the post-glenoid process. This is situated immediately lateral to the middle of the bulla.

The backward compression of the parts posterior to the glenoid, which is particularly noticeable in Bothriodon, is not apparent, and although the glenoids themselves are widely separated their relative position is retained and shows no indication of the outward and backward development found in the latter genus. The glenoids are not below the basi-cranial level, but dorsal to it as in Merycopotamus, nor are they close against the bullae, but are separated by grooves about 10 mm . in width. In these two respects the material differs from the usual condition occurring in Anthracotherium and Brachyodus.

In the holotype, the bulla of the right side is largely missing, whilst that of the left side is somewhat crushed. In the second example, however, the bulla of the right side is only slightly broken, whilst apparently retaining its original shape.

The bone is extremely fragile, and is held in position by the matrix which has filled the cavities inside. In length the bulla measures 52 mm ., and in breadth 24 mm . The ends are somewhat drawn out to give an elliptical shape, the axis of which is not quite parallel to the longitudinal axis of the skull, but diverges backwards from it at an angle of about $10^{\circ}$. At the postero-external border a process is given off which forms a very long tubular meatus, extending outwards between the postglenoid process and the paroccipital. This tube is badly damaged in each case, but it appears to have been some 30 mm . in length. In the third specimen the lateral compression of the fragment has caused the external walls of both bullae to collapse, giving them a concave outer edge. In length they agree very closely with that described, and in spite of the damage there can be no doubt that the general structure in each example was very similar.

## Upper Dentition (Pl. 2)

The incisors and canines are unfortunately lost, and only the root-cavities remain. On the broken anterior surfaces of the pre-maxillae large tooth cavities are visible, indicating very massive ist incisors. The 2nd incisor was greatly reduced, and separated from the ist by a diastema of about 30 mm . The canine was still further reduced, and was again separated from the 2 nd incisor by a $30-\mathrm{mm}$. space. It appears that both the canine and the lateral incisor projected obliquely forwards. The root cavity of the canine is separated by a diastema of 55 mm . from Pm. I. Pm.I-M. 3 are in closed series.

Pm.I.-This tooth is present only on the right side of the skull, and is incomplete. It consists of a main cone, from the apex of which a very pronounced crest extends down to the postero-external border. A similar, less pronounced crest probably extended to the antero-external point, but this is not preserved. A more obtuse crest connects the apex with the median part of the internal border. Thus the whole tooth is trihedral in section, with one slightly concave face to the outside, and one crest to the inside. The cingulum is only preserved on the postero-internal face, but it was probably continuous.

Pm.2.-In structure this tooth is very similar to Pm.I, though somewhat larger. The antero-external crest is complete, and shows a distinct tubercle at its middle point. The cingulum is visible all round the base of the crown, and is produced into a prominent shelf below the postero-internal face.

Pm.3.-The apex is broken in both examples of this tooth in the skull, but it appears to have been similar in structure to Pm.2, with the tubercle on the anteroexternal crest much more pronounced, forming a distinct style. The cingulum is again very well developed all round the tooth, particularly on the postero-internal border.

Pm.4.-This tooth is complete on both sides of the skull, and is also represented by two other isolated examples which probably belonged to a single individual, since they were found in association, and show the same degree of wear and preservation. The crown has the appearance of a single posterior lobe of a true molar, consisting of an outer and an inner cusp. In the worn state both cusps appear to be sharply selenodont, but in the unworn condition they appear to be somewhat more bunodont. The antero-external and postero-external crests of the outer cusp unite with the
cingulum to form massive anterior and posterior styles. The cingulum is very well developed on the posterior border, where it is separated from the cusps by a welldefined gutter. It persists on the inner and anterior surfaces, and the ends extend round the styles on to the external surface, where they slope downwards to the base of the crown.
M.I.-The first molar is represented on both sides of the skull, and also by two other specimens from the right side, both of which are in an unworn condition (Pl. 4, fig. 3). A deep transverse groove divides the crown into two lobes, separating the protocone, protoconule and paracone of the anterior lobe from the metacone and metaconule. The latter cusp is very much enlarged, and has the appearance of a hypocone. The cusps are all somewhat selenodont, on account of the well-developed antero-external and postero-external crests from the apex of each, and a somewhat rounded inner surface. An almost unbroken cingulum surrounds the base of the crown, and is particularly well developed on the anterior and internal borders, where it is separated from the cusps by a pronounced gutter. At the antero-external angle it gives rise to a strong parastyle, which is rather more compressed than in most Anthracotheres, and thus appears to project further. The posterior crest of the paracone and the anterior crest of the metacone meet at an acute angle, to form a strong and compressed mesostyle. The metastyle is almost absent, which gives the tooth a somewhat trapezoidal appearance. The antero-external crest of the metaconule projects partially across the transverse valley, to come almost into contact with the postero-internal margin of the paracone and the postero-external crest of the protoconule.
M. 2 and M. 3 are so similar in structure to M.I that no further description is necessary. In M. 3 the parastyle is more pronounced than in the preceding molars, and the posterior end is slightly less square. The size differences are shown in the table of tooth measurements. The enamel of all the teeth preserved shows the innumerable fine striations which, according to Schmidt and others, is characteristic of the African forms of Brachyodus.

An additional fragment of left maxilla (C.M. No. F. 36I8), bearing M. 2 and M. 3 fully erupted and slightly worn, was obtained from the red deposits of Gumba, Rusinga Island, in I94I. Structurally these two teeth are almost indistinguishable from those already described, and their slightly larger size is not thought to represent any specific difference. This specimen is of some importance, however, since it was obtained from a very low horizon in the Miocene succession on Rusinga, and one in which fossils are not abundant. The horizon is separated from the richer fossilbearing beds by a considerable depth of deposits and two major unconformities, and the occurrence of a single form both in the upper and lower series suggests that the time difference is of no very great significance. The measurements of the upper teeth, in millimetres, are on the opposite page.

Deciduous dentition.-The structure of two deciduous molars is shown in a fragment of the right maxilla of a juvenile animal bearing the crowns of three teeth (Pl. 4, fig. 4).

The posterior tooth in this fragment is an unworn molar, only partially erupted from the alveolus. In structure and size the tooth agrees closely with examples of M. 2 already described as $B$. aequatorialis. The crown of the preceding tooth is
missing, but the size of the root is compatible with that of M.I. Thus the tooth immediately in front of the broken root should be either Pm. 4 or Dm.4. The density of the bone is such that the results of X-ray examinations kindly undertaken by Dr. Hopkirk and also by Mr. Critchley were not very satisfactory, but there appeared to be no trace of an overlying tooth, as would have been expected if the doubtful tooth were Dm.4. In order to verify this, a small portion of bone was removed, revealing no indication of a succeeding tooth. It is however assumed that the tooth in question must be Dm. 4 , since the structure is quite unlike that of any Anthracothere Pm. 4 hitherto described.

The preceding tooth is therefore described as $D m .3$. In structure it is generally similar to Pm .3 of $B$. aequatorialis, consisting of a central cone from which a sharp crest extends to the postero-external angle. A very distinct tubercle is present in

| Skull |  | I. 2 | C | Pm. 1 | Pm. 2 | Pm. 3 | Pm. 4 | M.I | M. 2 | M. 3 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Right side | Length <br> Breadth | $-$ | $\begin{aligned} & 8 \\ & 4 \end{aligned}$ | $\begin{aligned} & 17+ \\ & 17 \end{aligned}$ | 22 $22+$ | $\begin{aligned} & 23 \\ & 24+ \end{aligned}$ | $\begin{aligned} & 2 \mathrm{I} \\ & 26 \end{aligned}$ | $\frac{3 \mathrm{I}}{?-3 \mathrm{I}+}$ | $\frac{32}{36-33}$ | $\frac{35}{38-34}$ |
| Left side | Length <br> Breadth | $\begin{aligned} & 9 \\ & 8 \end{aligned}$ | $\begin{gathered} 8 \\ 6.5 \end{gathered}$ | - | - | $\begin{aligned} & 23 \\ & 25 \end{aligned}$ | $\begin{aligned} & 2 \mathrm{I} \\ & 26 \cdot 5 \end{aligned}$ | $\frac{30}{30 \cdot 5-?}$ | $\frac{32}{35-32 \cdot 5}$ | $\frac{34}{37 \cdot 5-33}$ |
| Gumba teeth | Length <br> Breadth | - | - | - | - | - | - | - | $\frac{32}{39-36}$ | $\frac{35}{39-36}$ |

N.B.-The incisor and canine measurements are those of the root-cavities only. The double breadth measurements of the molars represent, on the left, parastyle to inner margin of anterior lobe, and on the right, mesostyle to inner margin of posterior lobe.
the middle of this crest. An anterior crest from the apex divides a little below its middle point, so that the front margin of the tooth consists of a flattened surface between the two subdivisions. The cingulum is continuous around the base of the tooth, and is particularly well developed on the postero-internal margin, where it forms a prominent shelf. In the holotype of $B$. aequatorialis described above, the three anterior premolars are so orientated that in each case the postero-external crest lies at an angle of about $80^{\circ}$ from the median axis of the palate. In the tooth under consideration this angle is only about $45^{\circ}$, whilst the size and proportions are also somewhat different.

Dm. 4 consists of a central anterior cusp, from the apex of which a slight crest extends to the antero-internal point, thence curving backwards to merge with a very marked cingulum. A more distinct crest extends outwards from the postero-external part of the cone, to unite with a massive antero-external style. A deep valley separates the anterior cusp from the higher median cusp, which is distinctly selenodont in form. The antero-external crest unites with the anterior style, whilst a more sharply defined postero-external crest appears to have joined an even larger posterior style. The posterior part of the tooth is missing, and it is thus impossible to determine whether it consisted of one or more cusps, or whether it comprised a very large
talon, but a well-marked impression of the posterior border suggests that the total length must have been about 30 mm . Thus the tooth consists of two main cones arranged longitudinally, whereas in all the examples of Pm .4 of $B$. aequatorialis it consists of two selenodont cusps arranged transversely.
M.2.-The second molar is almost identical in structure to those of $B$. aequatorialis, although the cusps appear to be slightly more slender. The posterior part of the tooth is somewhat obscured by the alveolus, from which it is incompletely erupted, so that the measurements are only approximate.

The infra-orbital foramen measures 10 mm . in height, and is situated 18 mm . above the alveolus, over the anterior cusp of Dm.4. Unfortunately this region is damaged in all examples of $B$. aequatorialis, so that no comparison of this feature can be made.

The measurements of the teeth, in millimetres, are as follows:

|  | Dm. 3 | Dm. 4 | M.I | M. 2 |
| :---: | :---: | :---: | :---: | :---: |
| Length | 19 | 30* | - | 33* |
| Breadth | 17 | 1722 | - | $34^{*}$ |

* Indicates that the measurement is approximate.

The cranial measurements, in millimetres, are as follows:
Total length . . . . . . . . . . . 559
Restored total . . . . . . . . . . . 620

Length of nasals . . . . . . . . . . . 185
Post-orbital constriction . . . . . . . . . 7 I
Pre-orbital constriction . . . . . . . . . 82
Orbital width . . . . . . . . . . . 122
Extreme width over post-orbital processes . . . . . . 172
Zygomatic breadth (approx.) . . . . . . . . 285
Bi-condylar width . . . . . . . . . . 106
Posterior extension of nasal aperture . . . . . . . I35
Probable maximum extension of nasal aperture . . . . . 195
Maximum pre-maxillary breadth . . . . . . . . 109
Length of right orbit . . . . . . . . . . 60
Depth of right orbit . . . . . . . . . . 46
Palatal breadth at Pm.I (int.) . . . . . . . . 63
Palatal breadth at M.I . . . . . . . . . 64
Palatal breadth at M. 3 . . . . . . . . . 6 I
Length of pre-molar series . . . . . . . . . 82
Length of molar series . . . . . . . . . . 93
Total length of Pm.-M. series . . . . . . . . 175

## Lower Dentition

A small tusk from Kiboko Island is thought to be the lower canine of this form. The tooth is in a bad state of preservation, and has lost the lower end of the root, so that the original length of the specimen cannot be determined. The enamel is almost entirely worn away by use, except on the external border. The anterior and posterior surfaces are obliquely worn, and produce a perfectly trihedral cross-section. The whole tooth is sharply curved, and appears to have projected for a distance of about 65 mm . beyond the alveolus. No other examples of the lower anterior teeth have yet been recovered.

The lower premolar-molar series is represented in two fragments of a single mandible from Rusinga Island (Pl. 3). Both the ascending rami are missing, and also the symphysis, but the two portions of horizontal ramus bear on the right side the second and third molars, and on the left side Pm.2-M.2. With the exception of M. 3 the teeth are fairly well preserved though considerably worn, but the bone is badly crushed, and in both fragments is broken immediately in front of, and behind, the teeth mentioned.

Pm. 2 consists of a main central cone with antero-internal and postero-internal crests, which produce a sharply selenodont surface in the worn state. A distinct posterior talonid is present, but the anterior part of the tooth is compressed into a sharp keel. In this respect the tooth differs from those of Fourtau's Masritherium (1920), where there is an anterior shelf as well as a posterior talonid. The cingulum is continuous and completely surrounds the tooth. As in $B$. onoideus, it is situated just above the root at either end of the tooth, but it rises sharply in the form of an inverted $V$ on the inner and outer margins. The posterior crest from the apex of the main cusp divides about half-way down, giving rise to a smaller crest, directed backwards down the middle of the posterior talonid, whilst the main crest folds sharply forwards along the inner margin of the tooth, uniting with the median internal apex of the cingulum. This forms a massive horizontal shelf, separated from the main body of the tooth by a distinct gutter. The anterior crest from the main cusp folds sharply backwards from a slightly lower level, and also unites with the cingulum a little below the apex. Thus the inner surface of the tooth has an irregular ridge across the middle (Pl. 3, fig. I). In most other species of Brachyodus these transverse ridges are absent, so that the inner surface of the premolars is almost smooth, divided at the base by the apex of the cingulum. B. onoideus shows the nearest approach to the condition described, but the arrangement is different. The summit of the cusp is situated further forward, with the result that the posterior crest descends almost directly to the median apex of the cingulum, whilst the fold from the anterior crest slopes straight to the apex. Thus the transverse ridge is a regular curve, and the inner face of the tooth is divided into two sub-equal parts. In the new species the anterior part is so much the greater that the posterior portion is almost negligible and appears merely as a part of the talonid. In B. africanus the transverse ridge is somewhat similar to that of $B$. onoideus, but is much less clearly marked.

Pm. 3 shows the same arrangement as Pm.2, except that the tooth is relatively broader and the talonid is more massive.

Pm. 4 is somewhat more quadrangular in outline, having a small anterior shelf in addition to the posterior talonid.

Another fragment of the right side of a horizontal ramus has Pm. 3 in place, with the roots of Pm. 2 and Pm.4. The tooth is rather less worn than the corresponding tooth in the larger specimen and shows that the cingulum is well developed all round the posterior talonid. Anterior to the roots of Pm. 2 the alveolus is constricted, and it is clear either that Pm.I was absent or that there was a diastema of some 30 mm . between Pms. I and 2.
M.I and M. 2 are very severely worn but they appear to have consisted of anterior and posterior lobes, each comprising an outer and inner cusp, without any traces
of talonids. The outer cusps of each lobe appear to have been very sharply selenodont, whilst the inner cusps were less so, but since the wear has united all these cusps it is impossible to be certain of their appearance. It seems, however, that at least in the worn condition, the anterior crest of the hypoconid extended diagonally across the median transverse valley, to unite with the metaconid.
M. 3 has lost almost all the enamel and only the dentine remains. The talonid is very long and narrow and is directed backwards, following the longitudinal axis of the tooth. The worn surface curves sharply upwards, so that at the posterior end of the talonid it is almost at right angles to the horizontal plane of the tooth.

The structure of both the second and third lower molars is more clearly seen in a fragment of a left horizontal ramus, found at Wakondu, Rusinga Island, in I947 (Pl. 4, figs. I and 2). This specimen has a somewhat damaged M.2, and an almost complete M. 3 in a slightly worn condition. M. 2 is rather less worn than that already described, but again the outer and inner cusps are united transversely, and the anterior crest of the hypoconid extends across the median transverse valley to join the metaconid.

In M. 3 the wear is less, and the anterior pair of cusps are united only by the posterior crest of the protoconid, which extends transversely to the postero-external point of the metaconid. The anterior arm of the protoconid curves across the front end of the tooth to unite at the extreme base with the antero-internal point of the metaconid. The enamel fold separating the anterior parts of the two cusps is blocked by a small tubercle which, with slightly increased wear, would connect the anterior crest of the protoconid with the antero-external point of the metaconid. A very similar condition is shown in the posterior lobe, where the entoconid appears to have had antero- and postero-external crests which have united through wear with the internal crests of the hypoconid, thereby enclosing an enamel pit between the bodies of the two cusps. The anterior arm of the hypoconid again extends diagonally across the median transverse valley towards the metaconid, but the dentine figures do not join. Posteriorly a large talonid projects backwards for a distance of I 9 mm . It appears to have consisted of a main central cone, from which an anterior crest extends forwards to the postero-median point of the posterior lobe. A second crest from the apex, curving inwards and forwards to meet the postero-internal point of the entoconid, appears to be derived from the cingulum. The latter is well developed across the anterior border of the tooth, but is absent at the sides of the anterior lobes, appearing again in the constriction between the posterior lobe and the talonid. The width of the first lobe is appreciably more than half of the total length of the tooth, which agrees with Fourtau's observation that this should be the case in Brachyodus africanus and Masritherium depereti.

The depth of the horizontal ramus is 74 mm . at the junction of M.I-M.2, and 83 mm . between M.2-M.3. A large mandibular foramen is present near the base of the lingual surface, below the anterior lobe of M.3.

The measurements (in millimetres) of the lower teeth, compared with those of the type specimens of $B$. onoideus and $B$. africanus, are on the opposite page.

A comparison of these measurements shows certain differences in the proportions of the teeth. In $B$. onoideus the teeth are, on the whole, longer than the Rusinga teeth, with the exception of M.3, which suggests that the talonid of the latter is
relatively shorter. The first and second molars of B. onoideus are relatively narrower than those of the new species, whilst all the rest of the teeth are broader. In the case of B. africanus only the third molar is broader in proportion, and the remaining teeth are slightly narrower. It seems, however, that the differences are so slight that their significance is doubtful.

| Tooth | Pm. 2 | Pm. 3 | Pm. 4 | M.I | M. 2 | M. 3 | $\begin{aligned} & \text { M.I- } \\ & \text { M. } 3 \end{aligned}$ | $\begin{gathered} \text { Pm. } 2- \\ \text { M. } 3 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Specimen <br> Rusinga paratype | $\frac{24}{15}$ | $\frac{26}{16}$ | $\frac{25}{17}$ | $\frac{25}{2 I}$ | $\frac{32}{23}$ * | $\frac{50}{2 \mathrm{I} \cdot 2 \mathrm{I} \cdot 10}$ * | 106 | 18I |
| Wakondu specimen | - | - | - | - | $\frac{35}{25}$ | $\frac{5 I}{28.25 .15}$ | - | - |
| B. africanus | $\frac{22}{13}$ | ? | $\frac{27}{17}$ | $\frac{25}{17}$ | $\frac{36}{24}$ | $\frac{5 I}{25 \cdot 24 \cdot 15}$ | II2 | 186* |
| B. onoideus | $\frac{23}{15}$ | $\frac{25}{19}$ | $\frac{26}{20}$ | $\frac{31}{17}$ | $\frac{37}{25}$ | $\frac{50}{27 \cdot 25 \cdot 16}$ | II8 | 192 |

The sign * indicates that the measurement is estimated only.

## Skeleton

The remainder of the material consists of isolated limb and foot bones, all of which were recovered from Rusinga Island. Although not definitely associated with any of the specimens already described, there can be little doubt that these examples belong to the genus Brachyodus, and it is therefore reasonable to assume that they also belong to the new species.

Humerus.-The distal ends of two humeri were found, which should perhaps be referred to this group. Both, however, are in such a poor state of preservation that they are of little value. The more complete specimen shows a very large supratrochlear foramen, but neither fragment is sufficiently well preserved for any measurement to be recorded.

Radius.-The proximal end of a radius (No. 835/47) from the Gumba red-beds is also included, since it was found in association with an astragalus (No. 830A/47) and various fragments of metapodials which are referred to this species. The facet for articulation with the humerus measures 85 mm . in width, with an obtuse crest dividing it into two unequal parts; the inner part being roughly quadrate in outline, measuring 4 I mm . from front to back and 48 mm . from side to side. The outer part of the facet is somewhat triangular, measuring 37 mm . from the crest to the outer apex. On the posterior surface, and at right angles to the facet for the humerus, there is an irregular facet for articulation with the ulna.

Carpus.-Three bones of the carpus are included, namely two left lunars and a right cuneiform. The lunar is high anteriorly, and rather narrow. The upper surface is occupied by a facet for the radius, which is mainly concave. A prominent ridge runs diagonally across this surface, from the antero-external corner to the middle of the internal surface. The inner border shows a facet for the scaphoid,
while the outer surface has two facets for the cuneiform, as in the hippopotamus. The lower surface is concave, and has two facets separated by a median ridge. The inner part articulated with the magnum, and the outer with the unciform. The median ridge becomes very prominent towards the front and forms a beak similar to that observed by Kowalevsky (1873) in the lunar of Hyopotamus.

The upper surface of the cuneiform is occupied by a facet for the ulna. The internal surface shows two facets corresponding with those on the external border of the lunar, with which they articulated. On the upper part of the posterior surface a flat facet shows the point of articulation of the pisiform. The lower surface is entirely occupied by a facet for the unciform. The outer border is produced into a massive process which projects outwards and downwards. The measurements of these bones in millimetres are as follows

| Anterior height | . | . | 60 | 67 | 46 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Maximum breadth | . | . | 38 | - | 44 |
| ", depth | . | . | 64 | 67 | 40 |

Metacarpal III.-One complete example of this bone is included, and the proximal ends of two others, all from the left side (text-fig. I, nos. I-3). The upper surface, which articulated with the magnum, is roughly triangular, with a flat surface to the front. The apex of this triangle is produced by a massive posterior process, and the whole surface is gently convex from front to back. On the anterior part of the upper internal surface there is a facet for the second metacarpal. There is no other facet on the internal surface, but a well-developed facet is present on the back of the posterior process, which may be a second point of contact with Mc. II, or may perhaps indicate an articulation with the posterior process of the magnum. On the anterior part of the upper external surface there is a small process with an upper and a lower facet lying at $90^{\circ}$ to one another. The upper facet apparently articulated with the unciform, while the lower facet articulated with Mc. IV. A second facet for Mc. IV is present on the external part of the posterior process. The shaft is roughened on either side almost throughout its entire length by the ligaments attaching metacarpals II and IV. The distal end of the bone shows a semi-cylindrical articulation, the posterior half of which is divided into two parts by a prominent median ridge. The measurements of this bone in millimetres are as follows:

| Maximum <br> length | Proximal end |  | Middle |  | Distal end |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Breadth | Depth | Breadth | Depth | Breadth | Depth |
|  | 47 | 48 | 37 | 23 | 41 | 40 |

Tarsus.-No bones of the hind limb have yet been recovered, but the tarsus is represented by four examples of the astragalus, three from the right and one from the left side; one left calcaneum; a right and a left cuboid; two naviculars from the right side, and a left external cuneiform.


Fig. I. Brachyodus. Left metacarpal III : I. anterior aspect ; 2. internal aspect; 3. external aspect.

The astragalus is somewhat similar in form to that of a hippopotamus, though distinctly more elongate. The proximal end shows the usual "pulley" shape, the outer flange being considerably the larger. The distal end of this outer flange curves sharply outwards to form a massive lateral process a little below the middle of the external surface. The posterior side of this process apparently articulated with the calcaneum. The main articulation for the calcaneum consists of a large posterior facet, which is slightly convex from top to bottom, and concave from side to side. An additional and adjacent facet extends from the lower external corner to the distal part of the external border. The distal end of the astragalus is mainly semicylindrical, divided by a sharp keel into two parts. From the crest of the keel to the outer margin the facet is flat and articulated with the cuboid, whereas inwards from the keel it is sharply concave from side to side and articulated with the navicular.

The measurements of these four specimens are as follows:

|  |  |  | A | B | C | D |  |
| :--- | :--- | :--- | :--- | ---: | ---: | ---: | ---: |
| External length | . | . | . | II5 | I25 | IO8 | I26 |
| Internal length | . | . | . | IO3 | II5 | 98 | - |
| Proximal breadth | . | . | . | 70 | 75 | 60 | - |
| Distal breadth | . | . | . | 70 | 80 | 75 | 85 |

The calcaneum is of considerable length on account of the greatly elongated tuber calcis. The latter is deep but slender, and splays out slightly at the end into two parts, separated by a wide groove. The main facet for the astragalus is triangular with rounded corners, one point extending inwards and one face to the outside. A large fibular process is present, which has a small facet on the inner side which articulated with the astragalus, whilst the whole of the rounded upper surface of the process articulated with the fibula. The distal extremity of the bone is produced to a sharp point, the inner part of which has a facet which appears to show a third point of contact with the astragalus, whilst the posterior part has a facet for the cuboid. The measurements of this bone are as follows:

| Length . $\quad$. |
| :--- |
| Depth at fibula facet <br> Depth at main astragalar facet <br> Depth of tuber calcis |

The upper surface of the cuboid is divided into the usual two facets. The outer part, for articulation with the distal process of the calcaneum, is slightly convex and slopes downwards from back to front. The inner part, which articulated with the astragalus, is sharply concave from front to back, and is slightly wider in front than behind. Posteriorly it rises into a very high process. A massive shelf projects from the inner wall of the bone, with two facets, separated by a deep groove, on its upper surface, both of which articulated with the navicular. Of these the posterior is the larger, whilst the anterior has an adjacent facet below and at right angles to it, which articulated with the external cuneiform. At the antero-internal corner another small facet shows a third point of contact with the navicular. The lower surface has a large rounded facet in front, which is very slightly convex, and articulated with metatarsal IV. An adjacent postero-external facet shows clearly that there was a well-developed metatarsal V .

Measurements in millimetres:

| Anterior height | . | . | . | . | . | . | . | 52 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Posterior ", | . | . | . | . | . | . | . | $97+$ |
| Maxmum breadth | . | . | . | . | . | . | . | $7 I$ |
| " depth | . | . | . | . | . | . | . | 78 |

The upper surface of the navicular is the converse of the inner distal part of the astragalus. The lower surface has a large anterior facet for the external cuneiform, with two smaller adjacent postero-internal facets for the middle and internal cuneiforms. The other facets on the external side of the lower surface show the converse of the two facets on the internal shelf of the cuboid. The third facet for the cuboid lies at the antero-external corner immediately below the astragalar facet.

Measurements in millimetres:


The external cuneiform is somewhat triangular in plan, with a flat surface to the front and a point to the back. The upper face is entirely occupied by a facet for the navicular, while the lower surface articulated with Mt. III. A facet at the postero-external corner shows the point of contact with the cuboid. The internal surface has three irregular facets, of which the upper must have articulated with the middle cuneiform, whilst the two lower facets may also have articulated with this bone or may possibly show a point of contact with the second metatarsal.

Measurement in millimetres:


The metatarsals are represented by one nearly complete specimen of the right Mt. IV; a second severely crushed but otherwise complete example from the left side; the proximal ends of a right Mt. IV and a left Mt. III, and the distal end of an indeterminate specimen (text-fig. 2, nos. $\mathbf{I}-5$ ). The proximal end of Mt. III has a large posterior process which produces a triangular surface for articulation with the external cuneiform.* On the upper internal surface two facets are present which show the points of contact with Mt. II. On the external surface a distinct pit is present, situated about 8 mm . from the top and 10 mm . from the front of the bone. This received the very prominent articular process which is present at the corresponding point of the inner wall of Mt. IV. The back of the large posterior process is missing, but it is clear from the examination of the fourth metatarsal that another point of contact with this bone was present.

[^0]

Fig. 2. Brachyodus. I-3. Right metatarsal IV: r. anterior aspect ; 2, 3. external and internal aspect of proximal end. 4,5 . Left metatarsal III : 4. internal aspect of proximal end ; 5. external aspect of proximal end.

Metatarsal IV also has a massive posterior process. The main part of the proximal surface is slightly concave and articulated with the cuboid. On the internal surface there is the strong process already mentioned, which projected into the cavity of Mt. III. Another small facet is visible at the postero-internal point of the posterior process, which also articulated with Mt. III. On the external surface of the bone a single large facet shows the point of contact with Mt. V. The distal end is very similar to that of the metacarpal already described, consisting of a semi-cylindrical surface, divided into two parts posteriorly by a prominent median ridge.

The measurements of the metatarsals, in millimetres, are as follows:

|  | $\underset{\text { length }}{\text { Maximum }}$ | Proximal end |  | Middle |  | Distal end |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Breadth | Depth | Breadth | Depth | Breadth | Depth |
| Mt. III | - | 46 | $48+$ | - | - | - | - |
| Mt. IV A | 222 | 44 | $44+$ | 42 | 24 | 47 | 42 |
| Mt. IV B | 222 | 48 | 6 I |  |  | ? | ? |
| Mt. IV. | - | 44 | 53 | (Breadth including articular process, 50 mm .) |  |  |  |

A number of phalanges was also obtained, of various sizes, and in varying degrees of preservation. The longest of these measures 90 mm . and the shortest 40 mm .

## Discussion

Miss Pearson (1927, p. 423) has shown that there is a tendency throughout the Anthracotheriidae towards an outward and backward movement of the glenoid surfaces. This development is not found as a continuous evolution from one genus to the next, but seems to have taken place separately throughout the different genera; thus the later forms are not necessarily the most specialized in this respect.

The skulls of Brachyodus show little compression in the basi-cranial region. The post-glenoid process is lateral to the bulla, which is only separated from the glenoid surface by a narrow groove, or may be directly in contact with it. Thus the external auditory meatus is behind the level of the post-glenoid. The paroccipital process of the exoccipital lies almost directly behind the post-glenoid process, from which it is separated by a considerable space. The basi-occipital is fairly broad and smoothly rounded. The facial region of the skull is usually only slightly elongated and the diastemata are therefore small. The upper molars lack the metastyle, but the parastyle and mesostyle are well developed and compressed.

The skull of Masritherium is as yet unknown, so that no comparison can be made, but the form of the mandible suggests a somewhat elongated snout. This genus differs from other members of the Anthracotheriidae in the aberrant incisors, of which only two remain in each jaw. From Fourtau's description of the teeth (I920) it appears that in other respects the genus is somewhat similar to Brachyodus. The genotype, Masritherium depereti, was an appreciably larger animal than Brachyodus aequatorialis described above.

In Bothriodon the compression of the basi-cranial region of the skull is the most marked, since the backward development of the glenoids is the greatest. The postglenoid process in this genus is projected backwards so that it lies lateral to the paroccipital process of the exoccipital, and considerably behind the bulla. The basi-occipital is narrow and keeled, and bears two large tubercles, separated by a shallow groove between the bullae, which are relatively close together. The glenoid surfaces are set wide apart, and consequently are separated from the bullae by a considerable space. The main body of the bulla is round, and according to Scott, only slightly inflated. At the posterior end there is a slight projection, and a posteroexternal process is given off to the external auditory meatus, which lies immediately above the post-glenoid process. The facial region of the skull is greatly elongated, so that there are considerable diastemata between the teeth. The crowns of the teeth are fairly hypsodont and the cusps selenodont. In the upper teeth the shape is more or less rectangular, on account of the presence of a well-developed metastyle, in addition to the parastyle and mesostyle. The latter are both quite wide loops and are not compressed and pointed as in Brachyodus. The anterior end of the space enclosed by the zygomatic arch is situated well behind the third molar, whereas in B. aequatorialis it projects forwards to the level of the mid-point of M.3. In profile the posterior part of the sagittal crest is convex.

The Rusinga specimens can be distinguished from the Anthracotherium and Bothriodon groups by reason of the great differences in the basi-cranial region of the skull, and certain differences in the dentition. It is possible that future discoveries of more complete examples of the genus Masritherium may reveal a closer similarity to the Rusinga specimens than is at present apparent, but with the limited material available it would be unwise to refer it to this genus without any knowledge of the lower incisors and canines, which should show the distinctive features.

The material can be distinguished from the Bugti group of the genus Brachyodus, since the teeth present all the characters which, according to Forster Cooper (1924), are features of the European and African forms of that genus, and from which the Bugti species differ. The four points specified by Forster Cooper are: the clearly developed cingulum; the fine striations of the enamel; the pointed mesostyle; and the trapezoidal outline of the molars.

It is unfortunate that owing to the usual lack of associated skeletal material the skeleton of Brachyodus is incompletely known. From the study of the foot bones of this collection, however, we may draw certain conclusions. The great length of the metapodials and of the phalanges shows that this animal, although large, was probably cursorial. This is also suggested by the elongation of the astragalus and calcaneum, besides other bones of the carpus and tarsus, which are not particularly adapted for supporting a great weight. An astragalus in the British Museum, assigned to $B$. onoideus, corresponds closely to those from Rusinga, whilst a mandible of the same species appears to be but little larger than the Rusinga fragments that are referred to B. aequatorialis. Thus, although the foot bones indicate an animal as large as, if not larger than a hippopotamus, it is perhaps not altogether unreasonable to suggest that they be referred to a species whose teeth are little more than half the size of those of the modern animal,

# Genus HYOBOOPS Trouessart 

## Hyoboops africanus (Andrews)

 (=Merycops africanus Andrews, 1914)Pl. 4, figs. 5-7

Type Locality.-Karungu, Kenya Colony ( $\mathrm{r}^{\circ} \mathrm{o}^{\prime} \mathrm{S}$ : : $34^{\circ} \mathrm{I} 5^{\prime}$ E.).
Material.-A small piece of right maxilla, bearing a much broken Pm.i; the tip of a left lower canine; an isolated right lower M.2; a fragment of mandibular ramus with remains of a right lower M. 3 and a complete left lower M. 3 (Pl. 4, figs. 5-7). All from Rusinga Island.

## Description

The upper premolar is too fragmentary to be described in great detail. It appears to have consisted of a single main cone, somewhat triangular in section, with a flattened crest to the front, another on the lingual side, and probably a very distinct postero-external crest. The cingulum is clearly marked round the anterior end, and also probably enclosed a small talon which is broken away. The measurements of this tooth in millimetres are as follows: Length 15 mm . (approx.). Breadth 12.5 mm .

## Lower Dentition

A very well preserved left lower M. 3 (834/47) was found in the red clays of Gumba peninsula at the western end of Rusinga Island. The tooth is slightly worn and agrees very closely with Andrews' description and figures of the type specimen. The antero-internal crests of the protoconid and hypoconid again extend right across the tooth in front of the metaconid and entoconid respectively, and the entoconid, which in the type was broken, is here complete and is a particularly high, pointed cusp similar to the metaconid. The loop of the talonid appears to be slightly more compressed bilaterally than that of the type, and lacks the penultimate conule on each wall, which are shown in Andrews' figures. The anterior lobe of the tooth is supported by a single long root, which is completely separated from the posterior roots from immediately below the crown. The root supporting the second lobe is parallel to the first and is united by a thin septum of dentine with that of the talonid, which is directed obliquely backwards at an angle of about $40^{\circ}$ from the anterior roots. This septum is partially broken away, but it clearly extended for the greater part of the length of the roots. The fine sculpturing of the enamel referred to by Andrews in his description of the type is again very distinct. The cingulum is entirely absent except at the anterior end.

A small fragment of right horizontal ramus (No. 866/47) bearing a very broken M.3, from Kulu-Waregu, and a weathered and damaged right lower M. 2 (No. 135/47) from the surface at Kathwanga, are also regarded as belonging to this species. M. 2 appears to have belonged to a somewhat larger animal, having a maximum breadth of 18 mm . at the posterior lobe, as compared with 16 mm . in the two third molars. The anterior part of the tooth is damaged, and the total length is thus uncertain, but must have been in the region of 30 mm . The structure, however, is very
similar to that of M.3, differing only in the absence of the talonid, the broad, flattened outer surface of the metaconid, and the presence of a strong cingulum around the posterior end.

In the Kulu-Waregu third molar the greater part of the hypoconid is preserved, but only an indication of the protoconid and talonid, whilst the inner cusps are entirely lost from root level. What little is preserved, however, agrees in structure and appearance with the other specimen, and the dimensions of both teeth are very similar to those of the type. The measurements, in millimetres, are as follows:

|  | Length | Breadth | Depth of ramus below mid: M. 3 | Thickness of ramus below mid: M. 3 |
| :---: | :---: | :---: | :---: | :---: |
| Type tooth: Karungu | 31 |  | 3 I | - |
| Gumba tooth | 32 | 16 | - | - |
| Kulu-Waregu tooth | 3 I | 16 | 31 | 22 |

A small piece of lower canine from Kathwanga, Rusinga, is provisionally included in this species on account of its general similarity to Andrews' description and figures of a specimen from Karungu. The section appears to be a somewhat more rounded triangle than in Andrews' example, and the enamel is smooth, but this is thought to be due to the greater degree of wear and damage. This tooth measures 24 mm . in thickness from front to back and 22 mm . from side to side.

## Hyoboops sp. indet.

Some additional fragments of Anthracothere remains were obtained from deposits near Ombo ( $0.0^{\circ} \mathrm{N} .-\mathrm{S} .: 34.0^{\circ} \mathrm{E}$.), on the north side of the Kavirondo Gulf. The material is much more severely damaged than that already described, and even the generic determination is open to doubt. As far as can be judged the teeth approximate to Hyoboops, but it is thought to represent a different species from Hyoboops africanus. The collection includes two fragments of maxilla of a single animal, each bearing the remains of two molars, but the enamel is almost entirely lost and their structure is therefore obscured. A third maxilla fragment, from the left side, shows the internal half of Pm.4, and the greater part of M.I. The inner cusp of the premolar is somewhat selenodont, and is surrounded at the base by a very welldeveloped cingulum, which is separated from the main cusp by a deep gutter, as in Brachyodus. The outer margin of the first molar is also broken, but the cingulum is well developed on the three remaining sides, particularly anteriorly. The crown of this tooth is somewhat more worn than that of the premolar, but it is clear that both were rather brachydont. The length of the premolar is io mm., and of the molar 17 mm . These measurements are taken in the middle line of each tooth and may not represent the original maximum.

An isolated upper molar appears to be M. 2 from the left side. Both the internal angles are lost and also the postero-external angle, but from what remains it appears that the cingulum was present on the anterior, internal and posterior surfaces, and absent from the external border. The cusps were sharply selenodont, and the
parastyle and mesostyle are not compressed, the latter forming quite a wide loop, such as is found in Bothriodon. The enamel is finely striated, but this is less marked than is usual in Brachyodus aequatorialis. This tooth measures 19 mm . in length and 2I mm. in breadth, the measurements being again taken at the middle in each case.

Two fragments of mandible, each bearing the remains of an unworn third lower molar, are also included. They appear to have belonged to a single animal, and to represent the same species as the other teeth. The talonid is lost in each case, but the anterior lobes of one specimen are preserved in good condition, though the internal cusps of the left tooth are damaged. The crowns of both teeth are very much more hypsodont than those of B. africanus or B. aequatorialis. The external cusps (protoconid and hypoconid) are selenodont, whilst the inner are pyramidal, with crests radiating from their summits. The anterior crests of the outer cones do not extend quite so far across towards the inner margin of the tooth as they do in H. africanus. There is a faint trace of the cingulum on the anterior borders of the teeth, and it is also visible as a very slight swelling at the bases of the outer cusps. On the inner surface it is absent altogether.

Another mandible fragment from the left side shows M. 2 and M. 3 in place, but in a very worn condition. The third molar is a trifle smaller than those described above, but the structure, as far as it can be seen, appears to be similar.

The greater parts of two right horizontal rami were also obtained from the same site. In both cases the teeth were severely worn during life, and both have suffered extensive post-mortem damage. In one of these fragments the body of the ramus is crushed and distorted almost beyond recognition. At the anterior end the root cavity of the canine is visible in the alveolus, separated by a space of 5 mm . from the broken root of Pm.I. Pm. 2 and Pm. 3 appear to have consisted of single, somewhat selenodont cones; Pm. 3 shows a distinct trace of a subsidiary tubercle on the posterior arm of the crescent. Pm. 4 was probably rather similar, but is too much worn to show any details.
M.I shows abnormal wear, being abraded almost to the level of the alveolus, and considerably below either Pm. 4 or M.2. M. 2 and M. 3 are also too much worn for any details of structure to be seen, consisting only of double ovals of dentine, without any trace of the individual cusps. The cingulum appears to have been only slightly developed throughout.

In the second mandible the body of the ramus is still mainly intact and seems to have retained its original shape. It is very much deeper and slightly more slender than that of the type specimen of $H$. africanus from Karungu, measuring 42 mm . in depth by 2 I mm . in thickness below Pm. 2, and 5I mm. in depth by 20 mm . in thickness below M.3, as compared with a depth of 3 I mm. below M. 3 both in the type of $H$. africanus and in the example described above from Kulu-Waregu. On the external surface the dental foramen lies under Pm.2, at rather below the middle height. On the internal surface of both specimens the posterior point of the symphysis is visible below Pm.2.

The fragment is broken anteriorly behind the canine, and the first two premolars were probably lost shortly after death; the root-cavities being clearly preserved in the alveolus. The two roots of Pm.I must have been almost completely
united, whilst those of Pm. 2 are clearly separated by a septum of bone. Pm. 3 consists of a single selenodont cone, with an accessory tubercle on each of the internal arms of the crescent. Pm. 4 appears to have been somewhat similar though more elongated, but much of the internal surface is broken away. M.I again seems to show abnormal wear, lying appreciably below the level of both Pm. 4 and M.2. The last two molars are even more worn than those of the preceding specimen, and much of the enamel is lost.

The remainder of the collection consists of an isolated right lower Pm. 4 and a small fragment of alveolus, again from the right side, bearing the inner half of Pm.4, and the greater part of M.2. The isolated premolar is almost complete, and very slightly worn, and the enamel pattern is therefore visible. The cingulum is well developed all round the base of the crown, and is separated from the main central cusp by a deep gutter at either end. It does not produce the inverted Vshaped ridge noted in the lower premolars of $B$. aequatorialis in the middle of the internal surfaces. The main cusp is selenodont, with crests from the apex to the antero-internal and postero-internal angles. Each crest gives rise to a very pronounced tubercle about half-way down; that of the posterior crest being set somewhat inwards, and producing a subsidiary parallel crest to the postero-internal angle. The posterior talonid is very well developed, whilst the anterior part of the tooth is more compressed. The enamel shows the usual fine striation which appears to be characteristic of the East African Anthracotheres.

In the remaining fragment all that is left of Pm. 4 agrees exactly with that just described. In M. 2 the outer cusps are sharply selenodont, the anterior crest of the protoconid extending nearly to the internal angle, but less markedly so than in the examples of Hyoboops africanus. The two inner cusps are mainly bunodont, but each has a distinct posterior ridge, directed straight backwards. The cingulum is well developed at the anterior end of the tooth, and extends round the outer margin of the protoconid. The hypoconid is missing, but it is probable that the cingulum was continuous on all but the internal border.

A lower milk molar, apparently Dm. 4 from the right side, was obtained from the same locality (Ombo), and is provisionally included in this genus. The tooth consists of three lobes, each composed of two cusps, of which the outer are selenodont while the inner are more bunodont. The cingulum is well developed on the anterior, outer and posterior surfaces, but is absent from the lingual side. The enamel is rather more smooth than that of the permanent teeth. This tooth measures $\frac{18}{7 \cdot 7-5 \cdot 8} \mathrm{~mm}$.

The measurements, in millimetres, of the permanent lower teeth from Ombo are on the opposite page.

## Discussion

It will be seen from the comparative measurements that the third molars of the Ombo collection are not appreciably smaller than those of Hyoboops africanus (Andrews). The second molars, on the other hand, are distinctly smaller than the one example referred to this species, and as far as can be judged all the teeth of the Ombo species were considerably more brachydont. In addition, the relative weak-
ness of the anterior arms of the outer crescents as compared with those of Andrews' species, together with the marked difference in the body of the ramus, suggest that the Ombo material must be specifically distinct. To describe a new species on the specimens available, however, would necessitate the selection of a type in which practically no details of structure are recognizable. It is therefore provisionally referred to an indeterminate species of Hyoboops until additional material permits a more exact determination.

The type specimen of Hyoboops africanus (Andrews) was obtained by Dr. Felix Oswald from one of the lowest horizons of the Karungu series of deposits, from which the remains of Brachyodus were also recovered. The Gumba tooth is again from the lowest level of the Rusinga series, from which one example of Brachyodus,

| $\begin{gathered} C \\ \text { root } \end{gathered}$ | $\underset{\text { Pm.I- }}{\stackrel{\text { Pm }}{ }}$ | $\begin{aligned} & \text { Pm.I } \\ & \text { root } \end{aligned}$ | Pm. 2 | Pm. 3 | Pm. 4 | $\begin{gathered} \text { M.I- } \\ \text { M. } \end{gathered}$ | M.I | M. 2 | M. 3 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\frac{6}{6}$ | 52 | $\frac{8}{5}$ | $\frac{13}{12}$ | $\underline{14}$ | $\frac{16}{12}$ | 62 | $\frac{12}{12}$ | $\frac{20}{17}$ | $\frac{31}{16.15 \cdot 9}$ |
| - | 53 | $\frac{10}{6}$ | II | $\underline{13}$ | $\frac{18}{\text { II }}$ | 59 | $\frac{10}{\text { II }}$ | $\underline{19}$ | $\frac{32}{14.15 .8}$ |
| - | - | - | - | - | - | - | - | $\frac{18}{?}$ | $\frac{26+}{15 \cdot 15 \cdot 7}$ |
| - | - | - | - | - | - | - | - | - | $\frac{29+}{15 \cdot 13 \cdot 8}$ |
| - | - | - | - | - | $\frac{16}{?}$ | - | $\frac{13}{?}$ | $\frac{20}{14}$ | - |
| - | - | - | - | - | $\frac{I 6}{I I}$ | - | - | - | - |

The above measurements represent length over breadth in each case. Most of the breadth measurements are only approximate on account of distortion and lack of enamel.
referred to above, was also obtained. Additional remains of Brachyodus have been found at the other localities from which fragments of $H$. africanus have been recovered on Rusinga Island. It is thus clear that the habitats of the two species must have been generally similar, and that they occurred together throughout at least the greater part of the period during which the deposits were formed.

There is at present no evidence to suggest that the fossil-bearing deposits of Ombo belong to an appreciably earlier or later period than those of Rusinga and other neighbouring localities. It is therefore of interest to note that hitherto all the Anthracothere remains from Ombo belong to a species not yet known to occur at any of the other sites, whilst the species already obtained from Karungu and Rusinga have not yet been found at Ombo.

It is to be hoped that future collecting in the same general area will yield material from which the distribution and relationships of the East African Anthracotheriidae may be more readily deduced.

## REFERENCES

Andrews, C. W. I899. Fossil Mammals from Egypt. Geol. Mag., London (4) 6: 481-484, pl. 23.
Andrews, C. W. 1914. On the Lower Miocene Vertebrates from British East Africa, collected by Dr. Felix Oswald. Quart. J. Geol. Soc. Lond., 70: 163-186, pls. 27-29.
Fourtau, R. 1920. Contribution à l'étude des Vertébrés Miocènes de l'Egypte, viii+i22 pp., 3 pls. Survey Dept., Cairo.
Forster-Cooper, C. 1924. The Anthracotheriidae of the Dera Bugti Deposits in Baluchistan. Palaeont. Indica (n.s.) 8, 2: 1-60, pls. 1-7.
Kowalevsky, W. 1873. On the Osteology of the Hyopotamidae. Phil. Trans. Roy. Soc. Lond., r63: 19-94, pls. 35-40.
Pearson, H. S. 1927. On the Skulls of Early Tertiary Suidae, together with an Account of the Otic Region in some other Primitive Artiodactyla. Phil. Trans. Roy. Soc. Lond. (B) 215: 389-460, 53 figs.
Schmidt, M. 1913. Ueber Paarhufer der fluviomarinen Schichten des Fajum, odontographisches und osteologisches Material. Geol. Palaeont. Abh., Jena (n.f.) II: 153-264, pls. 17-25.

## PRESENTED <br> 4-DEC 1951

## EXPLANATION OF PLATES

PLATE 1

EXPLANATION OF PLATE I
Brachyodus aequatorialis n . sp .
Fig. I. Skull, lateral view. Holotype, $\times \frac{1}{3}$.
,, 2. Skull, dorsal view. Holotype, $\times \frac{1}{3}$.


PLATE 2

## EXPLANATION OF PLATE 2

Brachyodus aequatorialis n. sp.
Fig. I. Skull, ventral view. Holotype, $\times \frac{1}{3}$
,, 2. Upper Dentition. Holotype, slightly reduced.


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## EXPLANATION OF PLATE 3

Brachyodus aequatorialis n. sp.
Fig. I. Left mandibular ramus, lingual view, approx. nat. size.
,, 2. Left mandibular ramus, occlusal view, approx. nat. size.
,, 3. Right mandibular ramus, labial view, approx. nat. size.
,, 4. Right mandibular ramus, occlusal view, approx. nat. size.

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BRACHYODUS AEQUATORIALIS
(2)

PLATE 4

## EXPLANATION OF PLATE 4

Brachyodus aequatorialis n. sp., Brachyodus sp. indet., Hyoboops africanus (Andrews)
Fig. I. Brachyodus aequatorialis. Left mandibular ramus with M. 2 and M.3, occlusal view, nat. size.
2. Brachyodus aequatorialis. Left mandibular ramus with M. 2 and M.3, lingual view, nat. size.
,, 3. Brachyodus aequatorialis. Right upper M.I, occlusal view, nat. size.
,, 4. Brachyodus sp. indet. Right maxilla with Dm.3, Dm. 4 and M.2, occlusal view, nat. size.
, 5. Hyoboops africanus (Andrews). Left lower M.3, lingual view, nat. size.
6. Hyoboops africanus (Andrews). Left lower M.3, occlusal view, nat. size.
,, 7. Hyoboops africanus (Andrews). Left lower M.3, labial view, nat. size.


BRACHYODUS and HYOBOOPS


[^0]:    * This fits well with the external cuneiform already described, and probably belonged to the same animal.

